Agricultural and Forest Meteorology 248 (2018) 432–440

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

Research paper

Effect of climatic and soil moisture conditions on mushroom productivity and related ecosystem services in Mediterranean pine stands facing climate change

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ARTICLE INFO

Keywords:
Fungi
Pinus
Global warming
Soil water balance
Weather
Non-wood forest products

ABSTRACT

Wild mushrooms contribute to a variety of ecosystem services. The expected warmer and drier conditions for the Mediterranean region as a consequence of climate change, are raising concerns about future mushroom productivity due to potential reduction of soil water availability for fungi. The aim of this study was to increase our understanding of the interaction between climate and soil moisture in relation to their impact on mushroom productivity in Mediterranean forests. Mushroom yield data were obtained from 28 permanent mushroom inventory plots intensively monitored in Maritime pine (*Pinus pinaster* Ait.) stands of northeastern Iberian Peninsula. Annual productivity of total, edible and marketed mushrooms was obtained from measurements conducted every week during the autumn fruiting season for years 2008–2015. Historical weather conditions were obtained through data interpolation from meteorological stations. Soil moisture data were obtained from continuous plot-level measurements. A process-based soil water balance model was used to predict soil moisture under two climate change scenarios, using the predictions of two different regional climate models. Mixed-effects models using either precipitation or soil moisture as predictors, in combination with other weather variables, were fitted to annual mushroom occurrence and yield data. Mushroom yield was primarily dependent on weather and soil moisture conditions during the same month, with the exception of precipitation, whose effects exhibited a one-month delay. High temperatures limited mushroom yield at the beginning of the fruiting season, but tended to enhance it towards the end. The analysis revealed no apparent negative effect of climate change on long-term mushroom productivity, but rather the opposite (i.e., predicted median productivity of marketed mushrooms for 2016–2100 was 23–93% higher compared to the current yield), mainly due to an elongation of the fruiting season arising from the combined effect of increased precipitation at the beginning of the season and warmer temperatures at the end.

1. Introduction

Wild mushrooms contribute to a variety of provisioning, cultural and supporting ecosystem services in the Mediterranean Basin and worldwide. On one hand, wild edible mushrooms represent an important food source and may be regarded as a key non-wood forest product (NWFP), especially in the Mediterranean basin where NWFPs are of particular socioeconomic importance (Boa, 2004; Croitoru, 2007). Indeed, in Mediterranean forests, the economic value of mushroom-based ecosystem services, can be much higher than the economic profit traditionally obtained from timber-oriented forestry (Palahí et al., 2009; Martínez de Aragón et al.,2011). Forest fungi also play a critical role in forest ecosystem functioning through their contribution to nutrient and carbon cycles (Mohan et al., 2014; Stokland et al., 2012).

Mushroom yield varies dramatically between years due to variation in the environmental factors that determine the duration of the fruiting season and the frequency of mushroom emergence (Alday et al., 2017; Boddy et al., 2014). Climate arises as the foremost important factor, with precipitation and temperature (and their interaction) having a major impact on mushroom phenology, yield and diversity (Bonet et al.,

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http://dx.doi.org/10.1016/j.agrformet.2017.10.024
Received 19 February 2017; Received in revised form 12 July 2017; Accepted 17 October 2017
Available online 05 November 2017
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2012; Büntgen et al., 2015; Kauserud et al., 2008, 2012; Ogaya and Peñuelas, 2005; Taye et al., 2016). However, the effect of climate on mushroom productivity is further modulated by the combined effect of site and soil characteristics and forest stand structure (Martínez-Peña et al., 2012; de-Miguel et al., 2014; Tomao et al., 2017). The interaction between these factors determines soil moisture, which may be regarded as an integrative driver of mushroom fruiting accounting for different processes resulting in a given mushroom productivity level.

Since fungal fruiting is mainly enhanced by humid and warm conditions, recent trends of temperature increase driven by climate change have been found to enhance yield and earlier mushroom emergence in humid temperate regions, while decreasing and delayed productivity has been observed under drier Mediterranean conditions (Boddy et al., 2014). Future hotter and drier conditions predicted by climate change models for the Mediterranean region (Allen et al., 2014), and the subsequent expected reduction in soil water availability, are likely to enhance drought stress and aridity in forest ecosystems, eventually affecting negatively mushroom productivity (Ágreda et al., 2015; Büntgen et al.,2015). Yet, given the uncertainty about precipitation patterns in climate change scenarios, the reverse could occur if early-autumn drought were not enhanced and the duration of the fruiting season were expanded due to increasing temperature in late autumn.

Climate-sensitive mushroom yield models are in short supply largely due to the lack of long-term monitoring of mushroom yield, especially in drought-prone environments such as the Mediterranean forests (Mohan et al., 2014), although some examples can be found in the literature (e.g., Bonet et al., 2012; Martínez-Peña et al., 2012; Hernández-Rodríguez et al., 2015). Moreover, mushroom yield models considering weather variables only, may fail to capture the actual water availability in the soil as they ignore soil water fluxes, especially those driven by evapotranspiration demands (Ágreda et al., 2015). Nevertheless, long series of soil moisture records in mushroom monitoring plots within forest ecosystems are scarce, since most studies on mushroom productivity are usually lacking such intensive measurements (Boddy et al., 2014). This may constitute a major drawback to our understanding of productivity patterns since modelers are then forced to use precipitation as a surrogate for a more proximal driver. Therefore, in view of the ecological and socioeconomic importance of mushrooms in the Mediterranean basin, a better understanding of the drivers of mushroom productivity is required in order to forecast the provision of the ecosystem services provided by mushrooms, especially within the context of climate change.

In this study, we aim at shading light on the climatic and soil moisture conditions driving mushroom productivity under typical Mediterranean conditions. Moreover, we intend to better understand the role of precipitation *vs* soil moisture in the development of predictive mushroom yield models, in particular: (a) which of the two factors results in models with higher predictive ability; and (b) how mushroom productivity predictions of models using either precipitation or soil moisture differ when projected towards future climates. We address these questions using data from a network of permanent mushroom inventory plots intensively monitored in northeastern Iberian Peninsula, and combining a process-based soil water balance model with mushroom yield statistical models. Analyses were done for three mushroom categories accounting for several ecosystem services; total mushrooms to deduce on the overall productivity (i.e., regulating/supporting services), and edible and marketed mushrooms to deduce on food supply and socioeconomic activity (i.e., provisioning and cultural ecosystem services). All models were projected to future climate conditions using downscaled, bias-corrected climate model predictions.

2. Materials and methods

2.1. Study area and mushroom inventory plots

The study area is located in the Natural Park of Poblet in Catalonia, North-East Spain (41° 21′ 6.4728 latitude and 1° 2′ 25.7496 longitude). The area is characterized by a coastal Mediterranean climate, with mean annual temperature of 11.8 °C, annual rainfall of 665 mm and a pronounced summer drought usually extending from mid-June to mid-September. A set of 28 permanent plots was established between 2008 and 2009 in 50-year-old, even-aged Maritime pine (*Pinus pinaster* Ait.) stands, representing a range of different conditions in stand structure, i.e., stand density from 446 to 2657 trees ha^{-1} and basal area from 20.9 to 81.7 $m^2 ha^{-1}$, as well as in elevation (594–1013 ma.s.l), slope (2–13%) and aspect. Mushroom inventory plots were 100 m^2 (10 m × 10 m) in size. Soil is siliceous and has franc-sandy texture. All trees were measured for diameter at 1.3 m breast height (DBH) in December 2010 and re-measured in August 2013.

2.2. Mushroom productivity sampling

In each plot, all mushrooms were collected every week between 2008 and 2015 (15 plots) and between 2009 and 2015 (13 plots) during the autumn fruiting season, i.e., from the beginning of September to the end of December, with the majority of the yield being concentrated in October and November. Mushrooms were species-identified, counted and weighted. Total annual yield was classified according to mushroom edibility and marketability categories. Edible mushrooms represented 87% of total mushroom yield, and marketed mushrooms represented, respectively, 43% and 50% of total and edible mushroom production. Marketed mushrooms consisted of seven species, 80% percent of the fresh biomass being represented by *Lactarius* group *deliciosus.* and 13% by *Macrolepiota procera*.

2.3. Meteorological data and climate change scenarios

Plot-specific daily weather variables were interpolated from Spanish meteorological stations [1990–2011], and from both Catalan and Spanish stations [1990–2015] following the DAYMET methodology (Thornton and Running, 1999; Thornton et al., 2000), as implemented in the R package 'meteoland' (De Cáceres et al., 2017). Daily precipitation, temperature (min, max and average) and relative humidity (min, max and average) were estimated for each plot by averaging the values of several meteorological stations with weighting factors that depended on the geographic proximity to the target plot. The estimate from each meteorological station was further corrected for differences in elevation between the station and the target plot. The high dependence of precipitation on local topography and the distance from weather stations might result in false-predictions of rain events that have not reached the plot, or miss-predictions of rain events which occurred locally at the plot but did not reach the weather stations. This may have an influence on both the estimated probability of occurrence for rain and the intensity of rain events.

Climatic projection data for the period 2016–2100 were obtained from the EU-CORDEX project, available at Earth System Grid Federation (ESGF; http://esgf.llnl.gov/). Daily precipitation, min/max temperature, relative humidity, radiation and wind speed data were assembled according to predictions of the CNRM-CERFACS-CNRM-CM5 global model under representative concentration pathways (RCPs) 4.5 and 8.5, later regionalized to Europe (at 11-km resolution) using CCLM4-8-17 and RCA4 regional dynamic models. As a result, we obtained four alternative climate change scenarios based on the combinations between the two RCPs and the two regional climate models. These predictions were downscaled by correcting for local topography using the 1990–2015 period as reference. Future projected values were corrected for biases calculated monthly for the reference period. In the case of precipitation, correction involved quantile mapping (Gudmundsson et al., 2012). All corrections were conducted using the package 'meteoland' (De Cáceres et al., 2017).

Table 1
Summary of the main data used.

Model Variables	Mean	SD	Minimum	Maximum
Total mushroom yield (kg ha^{-1} yr^{-1})	86.37	102.17	0.01	481.61
Edible mushroom yield (kg ha^{-1} yr^{-1})	74.92	97.79	0.00	459.45
Marketed mushroom yield (kg ha^{-1} yr^{-1})	37.09	72.63	0.00	452.24
Total mushroom occurrence (probability)	1.00	0.00	1.00	1.00
Edible mushroom occurrence (probability)	0.94	0.24	0.00	1.00
Marketed mushroom occurrence (probability)	0.70	0.46	0.00	1.00
August precipitation (mm)	12.45	10.92	0.00	35.28
September precipitation (mm)	49.42	32.92	0.21	111.73
October precipitation (mm)	58.13	62.39	6.88	235.37
November precipitation (mm)	101.43	74.52	0.28	208.06
September number of rainy days (days)	7.92	4.54	1.00	14.00
October number of rainy days (days)	8.00	3.36	4.00	14.00
November number of rainy days (days)	9.47	5.80	2.00	25.00
November mean temperature (°C)	8.53	1.86	3.98	11.96
December mean temperature (°C)	5.09	1.59	1.08	7.80
September mean maximum temperature (°C)	22.33	2.90	15.37	27.71
October mean maximum temperature (°C)	17.77	2.22	12.23	21.83
November mean minimum temperature (°C)	4.14	1.73	0.83	7.32
December mean minimum temperature (°C)	0.71	1.29	−2.68	3.03
September mean relative humidity (%)	67.02	4.18	59.32	76.24
September mean maximum relative humidity (%)	95.72	2.28	90.23	98.85
September mean soil moisture (% of field capacity)	0.48	0.12	0.24	0.81
October mean soil moisture (% of field capacity)	0.60	0.19	0.24	0.93

2.4. Soil moisture sampling and prediction

Volumetric soil content below-ground was measured using Decagon 5 TM probes (Decagon devices Inc., USA) in each plot. Soil sensors were placed in the middle of each plot, 12–15 cm below-ground, and measurements were recorded every minute and stored as 2-h average on a data logger EM50 (Decagon devices Inc., USA). Volumetric soil moisture was converted to percentage of moisture relative to field capacity using soil texture and Saxton's pedotransfer equations (Saxton et al., 1986).

Since soil moisture measurements had started in April 2013 and they overlapped only partially with the mushroom collection period, a process-based soil water balance model, available in the R package called 'medfate' (De Cáceres et al., 2015), was used to reconstruct the historical daily series of soil moisture and complete the soil moisture observations for the whole 2008–2015 period. The model requires forest stand characteristics, site and soil variables and meteorological series as inputs. Each individual tree was treated separately, and its height and leaf area index were estimated from DBH according to existing allometric equations for *P. pinaster* (Villanueva, 2004). Soil depth was described in the model using two layers: topsoil (0–30 cm) and subsoil (30–150 cm). Soil texture was available from plot sampling. Macro-porosity was estimated from sand content and bulk density (Stolf et al., 2011), and values of the latter variables were obtained from the Harmonized World Soil Database (FAO/IIASA/ISRIC/ISSCAS/JRC, 2009). We used interpolated meteorological series as weather input since this method proved superior to simple assignment of weather data from the closest station, when compared as an input for the soil moisture balance model (results not shown). Since the model does not simulate changes in forest structure, to account for tree growth we simulated soil water balance twice for each stand, using DBH measurements from the two forest inventories. Model predictions for the period prior to the first inventory (i.e., 2008–2010) and after the second inventory (i.e., 2013–2015) were obtained using DBH values from the first and the second inventories, respectively. Predictions for the period between the two inventories were obtained averaging the two simulations, using linear weights based on their relative proximity to each of the inventories.

Topsoil moisture model predictions were validated by comparing them with the field measurements based on the mean squared deviation (MSD) and its partitioning into three additive components; squared bias (SB), non-unity slope (NU) and lack of correlation (LC) (Gauch et al., 2003). The comparison was done using daily and monthly time-steps.

Since model predictions are sensitive to the proportion of fine roots in each soil layer, and this information was lacking, we calibrated these model parameters by determining the distribution of fine roots that maximized the fit to observed soil moisture data in each plot. Specifically, 100 model simulations were done for each plot varying the root proportion in the topsoil between 0.01–0.99 (the proportion of roots in the subsoil was its complement). We selected the distribution of fine roots corresponding to the lowest MSD between observed and predicted soil moisture. Wilcoxon tests indicated a statistically significant reduction in MSD between calibrated and non-calibrated fine root distribution. Finally, a dataset of monthly averages of soil moisture was constructed, incorporating field observations complemented by model predictions for the missing period. Daily meteorological data was also aggregated into monthly values before building mushroom productivity models.

The soil water balance model was also used to obtain soil moisture values corresponding to climate projections [2016–2100]. For these simulations, the proportion of fine roots and forest structure (taken from the second inventory) were assumed constant for simplicity.

2.5. Mushroom occurrence and productivity modeling

Annual mushroom yield models were developed for the fresh mass of total, edible and marketed mushrooms, using data from the 28 mushroom inventory plots. Monthly values of the following weather variables were used as predictors of annual mushroom yield: cumulative precipitation, number of rainy days, mean temperature, mean maximum and minimum temperature, diurnal temperature difference, mean relative humidity, as well as mean maximum and minimum relative humidity (Table 1). Predictors were selected only if their correlation with mushroom yield was statistically significant, biologically sound and in agreement with current scientific knowledge on forest and fungal ecology, while at the same time avoiding multicollinearity.

We fitted models having either precipitation-related variables or soil moisture variables as factors representing the availability of moisture for fungal fruiting. Thus, we differentiated between precipitation-based and soil moisture-based models by replacing precipitation variables (both cumulative precipitation and number of rainy days) by soil moisture variables. The fitting procedure was based on mixed-effects

modeling (Pinheiro and Bates, 2000) using plot random effects to account for between-plot differences. Year random effects were not considered since the productivity of a given plot is mainly driven by annual changes in the monthly weather variables.

The probability of occurrence of mushrooms of any species in a given plot and year was 1 (i.e., for every plot and year, at least some mushrooms emerged during the sampling period). However, when focusing on edible or marketed mushroom species, zero annual yield values occurred in several plots and years. This pattern becomes more prominent due to the stochastic nature of mushroom emergence and the rather small size of inventory plots, further increasing the probability for zero yield. Therefore, a two-stage modeling approach was used for modeling annual production of edible and marketed mushrooms, accounting for two separate states (de-Miguel et al., 2014; Hamilton and Brickell, 1983). The first stage aimed at estimating the probability of mushroom emergence using mixed-effects logistic regression (Eq. (1)) with a logit link function (Eq. (2)) based on binomially distributed data corresponding to the absence or presence of mushrooms. The second stage aimed at estimating mushroom yield in the log scale, conditional on the former probability of occurrence, using linear mixed-effects modeling (Eq. (3)). Snowdon's bias correction factor (Snowdon, 1991) was used when back-transforming model predictions from the log scale to the original productivity units (i.e., kg ha^{-1} yr^{-1}).

The final production models result from the multiplication of the probability of mushroom occurrence by the mushroom yield conditional on the probability of occurrence (Eq. (4)), thus reflecting a combined effect of two separate states able to reveal potential differences concerning the effect of weather and soil moisture variables within each state.

$$P(y=1|x)_{ij} = \pi(x) = \frac{1}{1 + e^{-[(\alpha_0 + a_{0i}) + \alpha X_1]}} \quad (1)$$

$$g(x) = \log\left[\frac{\pi(x)}{1-\pi(x)}\right] = (\alpha_0 + a_{0i}) + \alpha X_1 \quad (2)$$

$$log\,(yield_c)_{ij} = (\beta_0 + b_{0i}) + \beta \log(X_2) + \varepsilon \quad (3)$$

$$yield_{ij} = \pi(x) \times e^{\log(yield_c)} \times Snowdon \quad (4)$$

where P(y = 1|x) is probability of occurrence of edible or marketed mushrooms in plot i and year j, $(yield_c)_{ij}$ is yield (kg ha^{-1} yr^{-1}) conditional on the probability of occurrence of mushrooms, $yield_{ij}$ is total, edible or marketed mushroom yield (kg ha^{-1} yr^{-1}) in plot i and year j, α and β denote fixed-effects model parameters, a_0 and b_0 denote plot random effects, $\mathbf{X}_1$ and $\mathbf{X}_2$ are vectors of predictor variables, ε is residual following a normal distribution with mean equal to zero and variance equal to σ^2, and *Snowdon* is the correction factor of the back-transformation bias.

Model selection followed an iterative, systematic procedure based on forward selection of predictors upon fitting statistics, considering the significance of model parameters (t-value ≥ 2, p-value ≤ 0.05), likelihood-ratio tests and residual standard error, while avoiding multicollinearity. Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) were used for variable selection in order to prevent overfitting and construct parsimonious models. The predictive ability of logistic models was further assessed by computing their receiver operating characteristics (ROC) curve and the corresponding area under the curve (AUC). Yield models were further evaluated by partitioning their MSD in three additive components; SB, NU and LC (Gauch et al., 2003). All data analyses and model fitting were performed in R software 3.2.2 (R Development Core Team, 2015). Mixed-effects models were fitted using "glmer" and "lmer" functions of "lme4" package (Bates et al., 2014).

Future mushroom productivity was predicted based on the predicted monthly weather and soil moisture variables under the four climate change scenarios. To prevent illogical predictions in extrapolation from the empirical mushroom yield models, predicted weather conditions for the period 2016–2100 were truncated according to the minimum and maximum values observed for the corresponding weather variables during the historical period 2008–2015.

3. Results

3.1. Water balance model and soil moisture estimation

Soil moisture predictions of the water balance model matched reasonably well the values measured in the plots, with the single exception of plot #22, which exhibited higher MSD (Fig. S1 of Supplementary Materials). The high bias for this particular plot was probably caused by its extreme gross texture and high rock content (which might result from an unrepresentative soil texture sample) leading to very low water holding capacity and strong fluctuation of soil moisture values. Therefore, for this specific plot, we opted for discarding the predicted soil moisture values and rely on measured soil moisture only. The proportion of fine roots distributed between topsoil and subsoil was calibrated for each plot, reducing significantly the MSD values. As a result, the average MSD was 0.025.

3.2. Models for total mushroom production

The information about model parameter estimates and predictors of total mushroom yield are presented in Table S1 of Supplementary Materials. The precipitation-based model (residual variance 1.031, random effects variance 0.330) performed better than the soil moisture-based model (residual variance 1.690, random effects variance 0.287), and the root mean squared deviation (RMSD) was 83.2 kg ha^{-1} yr^{-1} and 98.7 kg ha^{-1} yr^{-1}, respectively. For both models SB was zero, and most of the error was derived from LC, which was higher in the soil moisture-based model, whereas NU was slightly lower in the latter model (Fig. 1).

In the precipitation-based model, the rainfall of September, together with the accumulated number of rainy days in September, October and November, had a significant positive influence on total mushroom yield. The combined effect of November and December's mean minimum temperature had a significant positive effect on mushroom yield, so that the higher the mean minimum temperatures the higher the yield.

The soil moisture-based model included a wider variety of predictors, compared to the precipitation-based model. Total annual

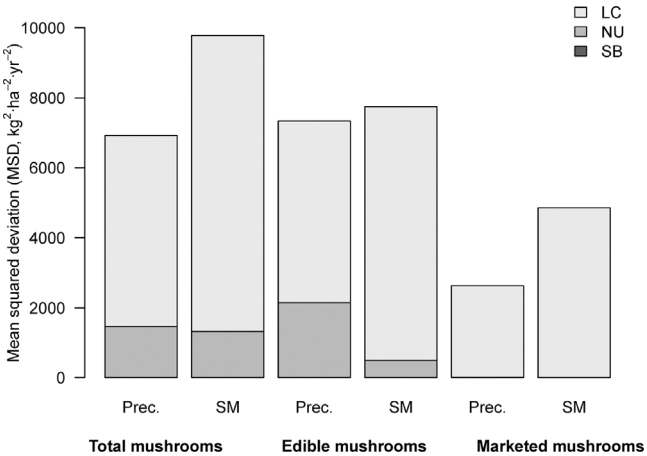

Fig. 1. Mean squared deviation (MSD) of precipitation-based (Prec.) and soil moisture-based (SM) mushroom yield models, for the three mushroom categories (total, edible and marketed), resulting from the difference between observed mushroom yield and model-based predictions. The MSD is partitioned in three additive components; Squared Bias (SB), Non-unity Slope (NU) and Lack of Correlation (LC) based on Gauch et al. [2003].

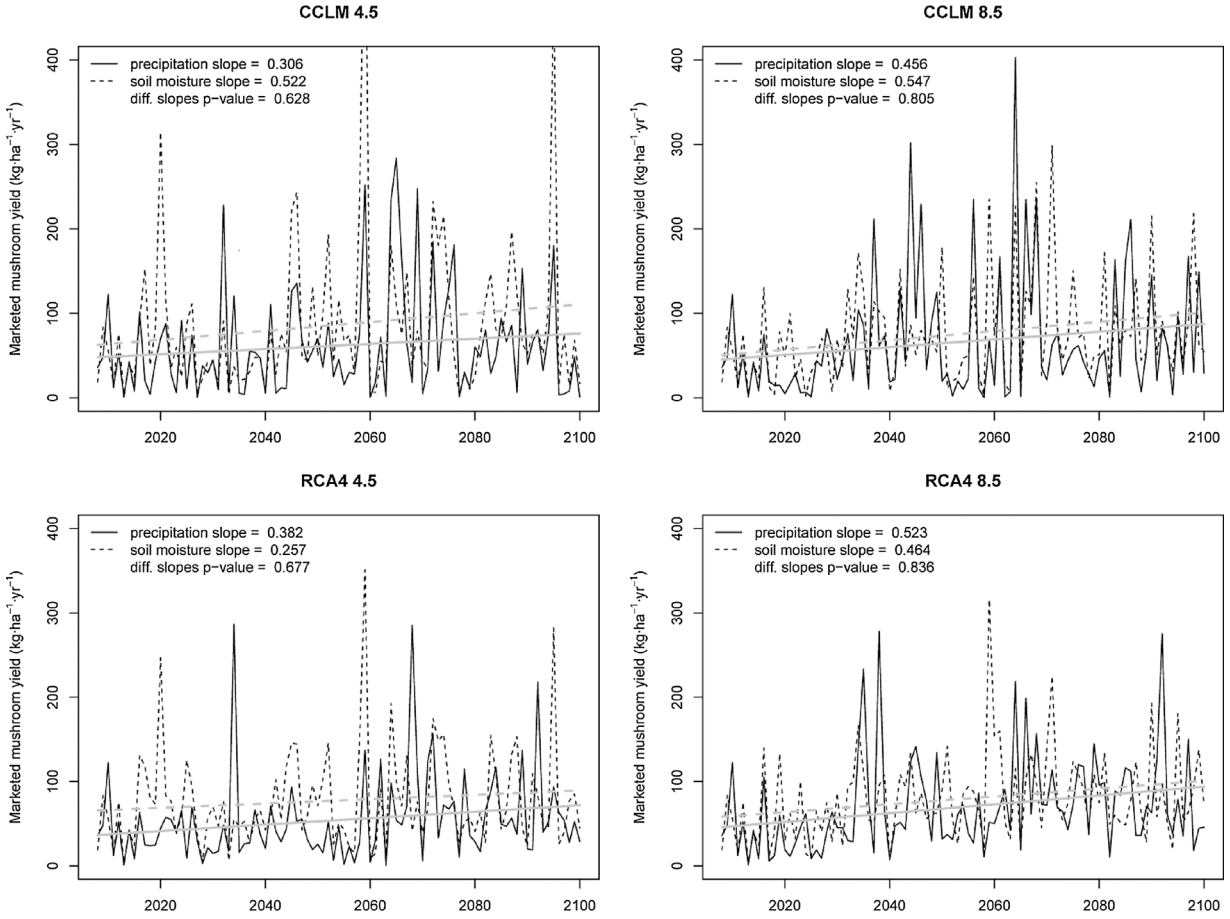

Fig. 2. Predicted annual productivity of marketed mushrooms under the four climate change scenarios according to the precipitation-based (black solid line) and soil moisture-based (black dashed line) yield models. The grey solid and dashed lines represent the overall trend of marketed mushroom productivity from 2008 to 2100 according for both yield models, respectively.

mushroom yield was positively correlated with soil moisture of October, the combined effect of November and December's mean minimum temperature, and the mean maximum relative humidity of September. Furthermore, the model revealed a negative effect of the sum of mean maximum temperatures of September and October, meaning that the lower the maximum temperatures of late summer and early autumn the higher the observed yield.

3.3. Models for edible mushroom occurrence and productivity

The information about the models of edible mushroom yield is presented in Table S2 of Supplementary Materials, for both probability of occurrence and yield conditional on occurrence models. The probability of occurrence of edible mushrooms in the precipitation-based model (AUC = 0.90) was positively correlated with the number of rainy days in October and the sum of the mean temperature of November and December. The yield conditional on occurrence model (residual variance 1.340, plot random effects variance 0.520) shared similar predictors with the total mushroom yield model. The root mean squared deviation (RMSD) was 85.7 kg ha^{-1} yr^{-1}, SB was zero and the majority of error was derived from LC (Fig. 1).

The probability of occurrence of edible mushrooms in the soil moisture-based model (AUC = 1.00) was positively correlated with the soil moisture in October and the mean minimum temperature of November and December. The yield conditional on occurrence model (residual variance 1.941, plot random effects variance 0.468) differed from the total mushroom yield model only in variable transformation. Moreover, it shared similar predictors with the probability of occurrence model with the sole addition of the positive influence of maximum relative humidity of September. The RMSD was 88.0 kg ha^{-1} yr^{-1}. SB was zero, the majority of error was derived from LC, and NU was lower compared to the precipitation-based model (Fig. 1).

3.4. Models for marketed mushroom occurrence and productivity

The information about the models of marketed mushroom yield is presented in Table S3 of Supplementary Materials, for both the probability of occurrence and yield conditional on occurrence. The probability of mushroom occurrence in the precipitation-based model (AUC = 0.96) was positively correlated with the number of rainy days in September, the rainfall in October and the mean minimum temperature of November. The yield conditional on occurrence model (residual variance 1.367, plot random effects variance 0.724) consisted of two main differences compared to the probability of occurrence model; an increasing-decreasing influence of the rainfall in October suggesting that extreme high values of precipitation might cause a decrease in the yield of marketed mushrooms, and a positive influence of November's mean temperature only. The RMSD was 51.3 kg ha^{-1} yr^{-1}. SB was zero, NU virtually zero, while the error was almost completely derived from LC (Fig. 1).

The probability of mushroom occurrence, according to the soil moisture-based model (AUC = 0.93), was positively influenced by the combined effect of soil moisture in September and October and the mean minimum temperature of November, while negatively affected by the mean maximum temperature of October. The yield conditional on occurrence model (residual variance 1.861, plot random effects variance 0.768) showed to be positively influenced by soil moisture of October and mean maximum temperature of November, while

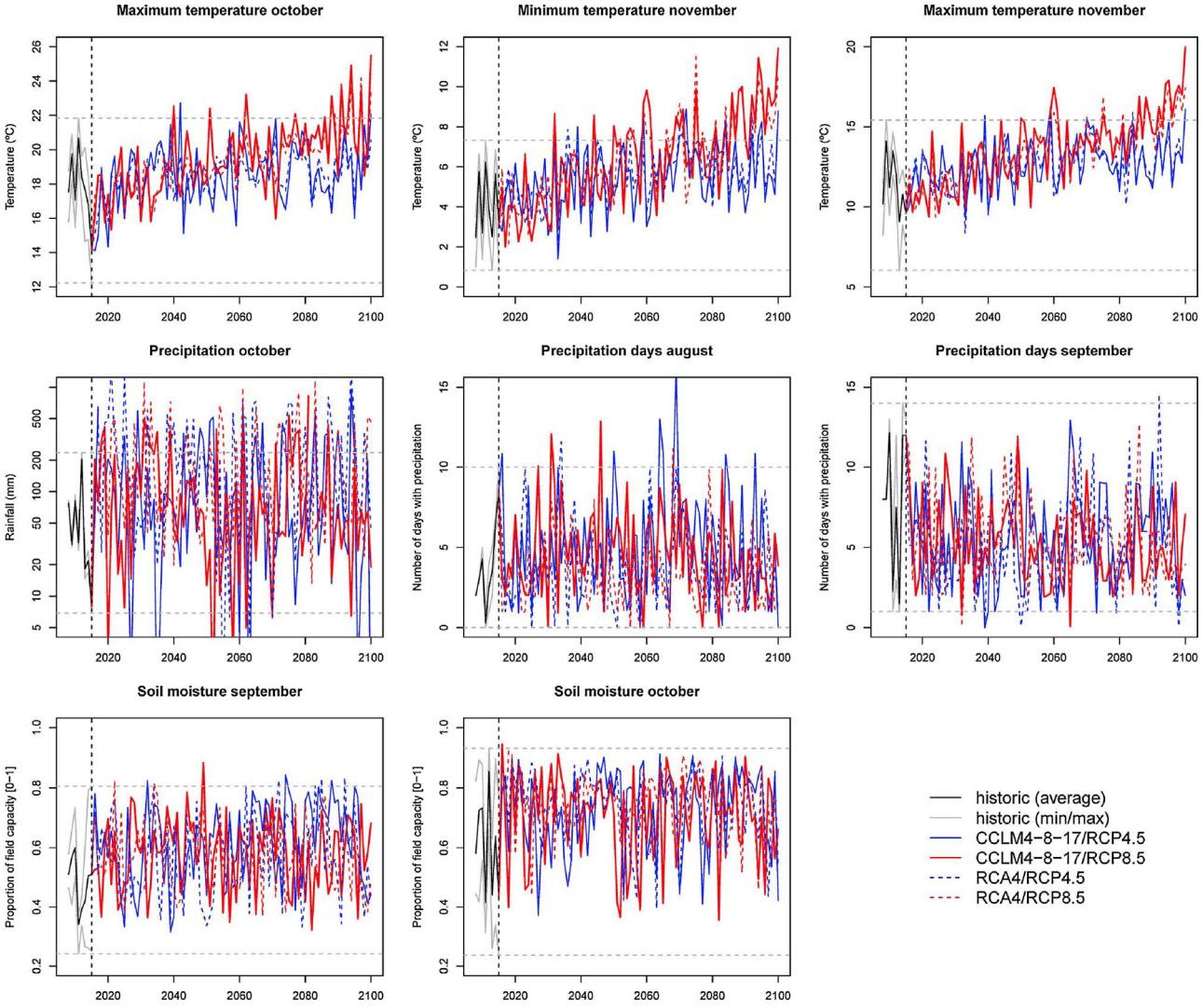

Fig. 3. Projected climatic and soil moisture predictors of marketed mushrooms for the period 2016–2100 under the two climate change scenarios (RCPs 4.5 and 8.5) and following the predictions of two regional climate models (CCLM4-8-17 and RCA4). Historic values during the mushroom inventory period [2008–2015] are also shown for comparison.

negatively affected by mean maximum temperature of October. The RMSD was 69.7 (kg ha^{-1} yr^{-1}). SB and NU were zero, while the whole error was derived from LC (Fig. 1).

3.5. Future mushroom productivity under climate change

Unexpectedly, the predicted mushroom productivity for the period 2016–2100 revealed a positive effect of climate change on long-term mushroom productivity. We found increasing mushroom yield for all mushroom categories under the four combinations of climate change scenarios and regional climate models (Fig. 2). A detailed inspection of the effect of climate change scenarios on the main predictors of mushroom yield revealed that, whereas autumn precipitation and soil moisture are expected to remain more or less stable (or even increase slightly) during the fruiting season along the 2016–2100 period, the temperatures are expected to increase, as compared to the historic period 2008–2015 (Fig. 3).

Soil moisture-based models resulted in higher mushroom productivity predictions as compared to the precipitation-based equations, although these differences were much smaller for the group of marketed mushrooms. We also found contrasting results between climate change scenarios and climate regionalization models in relation to the

Table 2
Medians of future[2016–2100] mushroom productivity (kg ha^{-1} yr^{-1}) as predicted by the precipitation- and soil moisture-based yield models according to the four climate change scenarios resulting from the two representative concentration pathways (RCPs) 4.5 and 8.5, and the regionalization conducted with the two alternative dynamic models CCLM4-8-17 and RCA4.

		RCP 4.5 [2016–2100]		RCP 8.5 [2016–2100]	
Mushroom group	Yield model	CCLM	RCA4	CCLM	RCA4
Total	Precipitation-based	72.00	52.67	70.12	73.59
	Soil moisture-based	251.55	306.57	178.84	290.93
Edible	Precipitation-based	57.33	43.11	59.55	59.55
	Soil moisture-based	174.18	239.70	137.90	223.79
Marketed	Precipitation-based	45.38	43.67	42.74	60.90
	Soil moisture-based	67.00	66.01	63.84	74.42

mushroom yield models (Table 2). Thus, we found that future mushroom yield, as represented by the median productivity predicted from precipitation-based models, was always higher in the most drastic RCP in terms of temperature change (RCP 8.5) when the RCA4 climate regionalization model was used, whereas differences between RCPs were minimal when using the CCLM4-8-17 model. Conversely, future mushroom productivity predicted from soil moisture-based models tended to be lower for RCP 8.5 than for RCP 4.5 regardless of the climate regionalization model, except for the case of marketed mushrooms when using the RCA4 model. For RCP 8.5, future mushroom productivity from both precipitation- and soil moisture-based models tended to be always higher for the RCA4 model than for the CCLM4-8-17 model. In contrast, for RCP 4.5, the RCA4 model resulted in lower mushroom productivity when coupled with precipitation-based models, whereas the CCLM4-8-17 model resulted in higher total and edible mushroom yield using soil moisture-based models.

4. Discussion

4.1. Differences between yield and occurrence models and between mushroom categories

Total and edible mushroom yield were related to the same set of predictors in both precipitation- and soil moisture-based models. This is logical since edible mushrooms represented 87% of total mushroom biomass. In contrast, marketed mushroom yield was related to a different set of predictors. Moreover, 93% of marketed mushrooms consisted of *L.* group *deliciosus* and *M. procera*, which implies that the latter models are mainly driven by the ecological requirements of these fungal species only. The predictors included in marketed mushroom models shifted one month earlier compared with those included in total and edible mushroom models. Namely, the precipitation-based model included August's precipitation and excluded November's, while the soil moisture-based model included the soil moisture of September in addition to October's. Furthermore, both excluded the temperatures in December, being the last month of the fruiting season. These results indicate on an earlier phenology of the marketed species and match the fact that *M. procera* fruit early in the season and is exclusively responsible for the marketed yield of September in our study area.

Models for probability of occurrence and models for yield differed in their predictors. Generally, yield models accommodated a larger number of predictors covering the extent of the whole fruiting season, while only a narrower time frame was required for the occurrence of mushrooms. Thus, regarding marketed mushrooms, the precipitation-based model for the probability of mushroom occurrence showed a dependence on the precipitation in September and October and the temperature in November, while an increase in yield resulted from the addition of precipitation of August, which may positively affect the early fruiting of *M. procera* in September. Another interesting difference was the increasing-decreasing effect of precipitation in October only present in the yield model. This suggests that while precipitation is essential for mushroom occurrence, the effect on the yield can turn negative in excessive wet conditions for some species (Boddy et al., 2014) which may be due to reduced soil aeration (Moore et al., 2008).

4.2. Effect of weather and soil moisture variables on mushroom occurrence and productivity

Precipitation and temperature variables were the most important predictors of mushroom emergence and yield. In the Mediterranean, mushroom production is limited in the beginning of the season (September-October) by high temperatures and low rainfall, that is, by a prolongation of summer drought. Thus, the extension of summer-like weather into the fruiting season diminishes the production (Büntgen et al., 2015). Fungal communities in Mediterranean ecosystems may already be experiencing a delayed phenology and reduced production for these reasons as a result of climate change (Boddy et al., 2014). On the other hand, in the end of the season (November-December), when precipitation and water availability in the soil are sufficient for mushroom fruiting, the production is often limited by low temperatures. Hence, cold temperatures in these months may be related to decreasing mushroom yield (Hernández-Rodríguez et al., 2015). While, in the literature, the effect of temperature on mushroom yield is reported as variable (Boddy et al., 2014), we found that there is no contradiction in having both positive and negative effects during a single fruiting season.

Interestingly, in most cases our models indicated that the mean maximum and minimum temperatures for September-October and November-December, respectively, are more significant predictors than mean temperatures. While agreeing with previous research regarding a non-linear effect of temperature on fungal development (Boddy et al., 2014), these findings also suggest a greater sensitivity of mushroom fruiting to daily extreme temperatures over mean temperatures, so that the exposure to extreme weather events might result in a greater inhibition of observed production.

The number of rainy days in a particular month often revealed as a more significant predictor than the cumulative rainfall since it accounts for both the amount of precipitation as well as for its temporal distribution. In all models, precipitation (i.e., cumulative rainfall and number of rainy days) exhibited a one-month time lag in its correlation with mushroom productivity, that is, it became a significant factor affecting one month before the start of the mushroom season, and ceased to be significant one month before the end of the season. This is in agreement with previous research indicating a one month delay in the effect of rain events on mushroom yield in the Mediterranean (Bonet et al., 2012, 2010; Martínez de Aragón et al., 2007; Taye et al., 2016).

In all our models, soil moisture appeared as a significant mushroom predictor one month later than precipitation did, thus matching the initiation of fruitbody production. Soil moisture follows rainfall event's intensity (Ogaya and Peñuelas, 2005), and showed a positive correlation with precipitation of the same and previous month. Nevertheless, maximum relative humidity, and not soil moisture, was significant in the month prior to fruiting (probably due to high correlation with precipitation), indicating that precipitation is probably influencing mushroom yield mainly by increasing soil moisture. The delay between precipitation events and mushroom yield might be explained by the necessity to first acquire enough fruiting potential before the initiation of fruit bodies (Krebs et al., 2008; Salerni et al., 2002).

It is worth highlighting that our data also showed an off-season effect of weather on mushroom productivity, exhibiting a highly negative relationship between precipitation in March (and to lesser extent in the whole spring) and autumn mushroom productivity. However, we could not find any support in the literature for such negative effect. On the other hand, spring precipitation was negatively correlated with autumn precipitation, an accepted fundamental driver of mushroom fruiting in the autumn season. Moreover, carbon from photosynthetic activity arrives to symbiotic fungi within days (Högberg et al., 2008; Leake et al., 2001). For all these reasons, we disregarded the negative effect of March precipitation on autumn mushroom yield as a statistical artifact rather than a true effect, further raising skepticism regarding such an off-season effect on mushroom productivity, reported in previous research (e.g., Primicia et al., 2016). A similar statistical artifact occurred regarding the effect of soil moisture on mushroom yield. During the colder months of the fruiting season (Nov-Dec), high values of soil moisture were associated with low mushroom yield, not because of a true negative effect of soil moisture, but rather due to the effect of low temperatures, which decrease soil drying rates but also inhibit fungal fruiting. This interaction produced an illogical negative correlation between soil moisture and mushroom productivity. In consequence, although soil moisture is known to be a crucial driver of fungal development and fruiting, its effect in our models was limited to rather warm months solely (i.e., Sept-Oct).

4.3. Climate change and mushroom productivity

Previous research has raised concerns about the potential negative effect of climate change on future mushroom productivity, with strong implications on the provision of mushroom-based ecosystem services related to the socioeconomic activities surrounding mushroom picking and trade. Indeed, some studies have highlighted that mushroom productivity in Mediterranean ecosystems may be experiencing a sharp drought-induced decrease (Ágreda et al., 2015; Boddy et al., 2014) due to delayed phenology in the autumn season (Büntgen et al., 2015; Kauserud et al., 2012). This could affect more severely the group of marketed mushrooms since, as described above, some of the earliest edible species to fruit belong to this category. However, our results reflect a different trend, namely, that mushroom productivity in the study area may be enhanced under most of the climate change scenarios analyzed. The predicted positive impact of global warming on mushroom productivity arises from the effect of the main variables that drive mushroom occurrence and yield, which results in an elongation of the mushroom fruiting season rather than a shortening associated with a delayed phenology. Thus, in the evaluated scenarios (i.e., ranging from the less severe RCP 4.5 to the most drastic RCP 8.5), the amount of rainfall at the beginning of the season is predicted to remain more or less stable (or even increase slightly) until 2100, despite the inter-annual fluctuations. Although the climatic models also predict a slight reduction of the number of rainy days, therefore resulting in more intense rain events, in most cases this does not seem to be relevant enough to hinder mushroom productivity. Furthermore, the models predict increased temperatures at the end of the fruiting season, when cold weather conditions often inhibit mushroom emergence and growth, which would contribute to expanding the mushroom fruiting season. Interestingly, these effects are more exacerbated in the most drastic RCP 8.5, which in general results in higher expected mushroom productivity for the period 2016–2100. However, there is uncertainty about the actual extent of these effects inasmuch as, in addition to the intrinsic uncertainty associated to any global warming scenario, we found considerable differences (and in a few cases, opposite trends) in future mushroom yield predictions among the two models (CCLM4-8-17 and RCA4) used for the regionalization of the global climate model predictions. Moreover, the response of mushroom fruiting to climate change may be fungal species-specific according to the ecological requirements of each taxon.

4.4. Causal drivers versus predictive variables of mushroom productivity

It is worth highlighting the relevance of distinguishing between causal drivers and predictors of mushroom productivity. Precipitation is not the most proximal causal driver of fungal development compared to soil moisture, but precipitation variables proved more significant predictors of mushroom productivity. Thus, it seems that rain events integrate several important causal drivers, such as a positive influence on soil moisture and relative humidity, and negative or positive effect on temperature. Soil moisture-based models, which included soil moisture instead of precipitation variables, had lower explanatory power than precipitation-based models. Nevertheless, soil moisture-based models provided a more profound insight into mushroom production dynamics. Since soil moisture did not correlate as strongly with other variables as precipitation did, model selection led to the inclusion of predictors that were not selected in the precipitation-based models, and sharpened the effect of others. For example, soil moisture-based models refined the negative effect of low mean temperatures in November and October, revealing the high sensitivity of edible mushroom emergence to extreme temperatures by replacing the predictor of mean temperature by minimum temperature. Similarly, the negative effect of maximum temperatures in September and October on total mushroom production, and the positive influence of relative humidity in September on total and edible mushroom yield only appeared significant when accounting for soil moisture instead of precipitation in the models. Therefore, our results suggest that the inclusion of precipitation as a predictor, while having great predictive ability, may obscure the effect of several mushroom fruiting drivers because of the correlation between precipitation and these drivers. On the other hand, precipitation-based models may be used when the main aim is yield prediction.

Acknowledgments

This work benefited from the Erasmus Mundus Master Program MEDFOR (Mediterranean Forestry and Natural Resources Management) which provided a scholarship to the first author. Sergio de Miguel was supported by the European Union's Horizon 2020 MultiFUNGtionality Marie Skłodowska-Curie (IF-EF No 655815), Miquel De Cáceres benefited from a Ramon y Cajal fellowship (RYC-2012-11109), and José Antonio Bonet benefited from a Serra-Húnter Fellowship provided by the Generalitat of Catalunya. Additional funding came from the research projects MYCOSYTEMS (AGL2015-66001-C3-1-R − MEC Spain) and FORESTCAST (CGL2014- 59742-C2-2-R), and from the European project StarTree (No. 311919). Special thanks to Mr. Antoine Cabon for his assistance with R software.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2017.10.024.

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